Heredity (2020) 124:313–324
https://doi.org/10.1038/s41437-019-0274-3

the geneticssociety

ARTICLE

Handedness heritability in industrialized and nonindustrialized societies

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Received: 26 December 2018 / Revised: 9 September 2019 / Accepted: 12 September 2019 / Published online: 10 October 2019

Abstract

In modern societies, there is a decreased usage of traditional weapons to settle interpersonal or inter-group disputes compared to usage in traditional societies, possibly affecting the frequency-dependent selection on the handedness polymorphism. Another societal difference is the extensive automation of hard manual labour (including agriculture) in industrialized societies, relaxing the selection for hand specialization. Thus, selection of handedness is likely to differ between traditional and modern societies. As heritability determines the relative speed of evolutionary dynamics, handedness heritability was compared between industrialized and non-industrialized societies. First, individuals were sampled from a non-industrialized area in Indonesia, where violent conflicts are relatively frequent and tribal wars have been prevalent recently. Handedness was recorded directly or indirectly for 11,490 individuals belonging to 650 independent pedigrees, and handedness heritability was estimated using a pedigree-based animal model. Second, estimates of handedness heritability derived from published sources were collected to compare heritability estimates, accounting for various confounding variables. Non-industrialized countries displayed a significantly higher heritability value ($h^2 = 0.56$) than that of industrialized countries ($h^2 = 0.20$). Heritability decreased with time along the twentieth century in industrialized countries, independently of the frequency of left-handedness, and independently of the method used to measure handedness. In conclusion, the data are consistent with a decrease in handedness heritability following the industrialization process and/or the associated decrease in violence using traditional weapons. The difference in heritability between industrialized and non-industrialized countries suggests that selection of handedness is thus likely to differ between traditional and modern societies.

Introduction

Since prehistoric times, both right- and left-handed individuals have been ubiquitous in human populations, exhibiting geographical frequency variations (Dellatolas et al. 1991; De Agostini et al. 1997; Llaurens et al. 2009; McManus 2009; Raymond and Pontier 2004). A polymorphism maintained in all populations of a given species can happen for a neutral trait but is easily lost by genetic drift; therefore, at least some populations lose the polymorphism. The fact that the polymorphism of handedness is maintained in all human populations suggests that handedness is not a neutral trait and that some selective forces are maintaining this diversity. Directional selection, if acting alone, would lead to the fixation of the advantageous morph and eliminate the polymorphism. The ancient and ubiquitous polymorphism observed for handedness (Faurie et al. 2016) suggests that balancing selection is influencing this trait. This balancing selection could result from a situation-dependent benefit, such as a negative frequency-dependent selection (Raymond et al. 1996). Data have suggested that left-handedness, as the rare hand preference, could represent an important strategic advantage in fighting interactions. This notion has been largely supported by sport data (Brooks et al. 2004; Faurie and Raymond 2013; Goldstein and Young 1996; Loffing et al. 2012a, b); video experiments have shown that it is more difficult to predict the outcome of an action performed by a left-hander than it is by a right-hander, and this difference is attenuated,

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or even reversed, by specific training (Loffing et al. 2012b; Schorer et al. 2012). In addition, the correlation observed in traditional societies between the frequency of left-handers and the rate of homicide further suggests a frequency-dependent advantage of left-handers in violent interactions (Faurie and Raymond 2005, but see Faurie and Raymond 2013 and Groothuis et al. 2013). However, the fact that left-handedness never occurs at a frequency close to 50% (Faurie et al. 2005; Raymond and Pontier 2004) indicates that some evolutionary costs could be associated with left-handedness (Billiard et al. 2005). In Western societies, this cost has often been attributed to the technological environment, with asymmetrical artefacts being dangerous for left-handers (Aggleton et al. 1993; Coren 1989; Daniel and Yeo 1994). However, the frequency of left-handers is also far from 50% in any traditional society, suggesting the existence of costs in non-industrialized environments as well (Faurie and Raymond 2005, see also Ghirlanda et al. 2009).

In modern societies, the type of violence has radically changed with the introduction of modern weapons, with the consequence that no differential advantage of left-handers is expected anymore (with the exception of interactive sports, a restricted form of ritualized violence not using modern weapons). Another factor affecting handedness in industrialized societies is the extensive automation of most manual labour, including agriculture. Machines are now replacing a large part of the previous manual load, thus reducing hand usage and importance of hand specialization. Now, the majority of individuals do not use their arms and hands intensively for highly specialized tasks on an everyday basis (usage of keys, mouse, comb, hairdryer, phone, etc. do not require a very high and intense manual specialization). This general decrease of specialized and demanding manual tasks in the daily life of modern societies probably explains the secular decline of handgrip strength and, more generally, of muscular strength components, observed during the last century in countries such as the US, Canada, Denmark, and Spain (Malina 2004; Moliner-Urdiales et al. 2010; Silverman 2011). As a result, in industrialized countries, for a given manual action, each individual shows a preference for the use of one hand, although it is not always the same hand for two different actions (Salmaso and Longoni 1985). This notion suggests that right- or left-handed is not a general category but rather is defined as a function of the task, explaining why indexes have been often developed in industrialized countries to measure handedness, such as the one derived from the Edinburgh Handedness Inventory (Oldfield 1971). For the countries not affected by the process of extended mechanization, a higher level of hand specialization is expected. The only available comprehensive study was performed in Indonesia, where a strong correlation between the different tasks has been found, suggesting that handedness could be considered a general category (Nurhayu et al. 2018).

Selection of handedness is thus likely to differ between traditional and modern societies. As no direct frequency-dependent advantages associated with left-handedness are known in modern societies, it is expected that the frequency of left-handedness has decreased due to its fitness cost, as homicides and violence are no longer driven by traditional weapons. Societies displaying a traditional type of violence are becoming scarce, although some were still studied during the twentieth century (e.g., Chagnon 1988; Downs 1955; Harrison 1995). The general decrease in traditional violence during the twentieth century is attributable to pacification imposed by colonization or by higher state control, particularly over remote areas, and to a shift to other types of violence through the introduction of modern weapons.

When selection is present, the relative speed of evolutionary dynamics is determined by heritability (Falconer 1960; Lynch and Walsh 1998). It has long been known that in humans, handedness is heritable. This fact has been shown in cross-fostering studies (Carter-Saltzman 1980; Hicks and Kinsbourne 1976; Longstreth 1980; Saudino and McManus 1998), parent−offspring resemblance studies (Chamberlain 1928; Rife 1940; Coren and Porac 1980; Gangestad and Yeo 1994; Hicks and Kinsbourne 1976; McKeever 2000), twins studies (Medland et al. 2006, 2009; Sicotte et al. 1999), and a genetic association study (Armour et al. 2014). The measure of heritability has been analysed several times during the last hundred years (e.g., Annett 1973; Chamberlain 1928; Coren and Porac 1980; Falek 1959; Hicks and Kinsbourne 1976; McGee and Cozad 1980; McKeever 2000; Merrell 1957; Rife 1940; Risch and Pringle 1985; Warren et al. 2006), although the various resulting estimates are probably not directly comparable. First, handedness was measured differently across the studies, and some of the tasks considered, such as writing handedness, are prone to cultural influences (Shimizu and Endo 1983; Teng et al. 1976), thus probably affecting the estimate of heritability. Second, the samples used to estimate the handedness heritability were from different places, different years or different centuries and were not always representative of the general population. Heritability is not an intrinsic property of a trait: it varies with phenotypic and additive genetic variances and thus can vary across populations and across generations (Falconer 1960; Lynch and Walsh 1998). Therefore, the interpretation of the variation in the published estimates of handedness heritability is unclear. In addition, most heritability estimates published thus far seem to concern only samples from industrialized countries.

Here, we sampled individuals from a non-industrialized area, Flores and Adonara Islands from Indonesia, where violent conflicts are relatively frequent and tribal wars were still prevalent very recently. We recorded their self-declared handedness and the handedness assignment of their kin members. The resulting information on pedigrees allowed the use of modern tools to estimate handedness heritability for these populations. Then, we collected all the published estimates of handedness heritability, or calculated them using raw data when available, to analyse the variability of heritability estimates as a function of the country type (industrialized or not), taking into account the method of measuring handedness, the left-handedness frequency, and the sampling year.

Materials and methods

Sampling

Sampling was performed on the islands of Flores and Adonara, Indonesia. On these islands, people generally work in traditional agriculture. Violence is relatively frequent, either as ritualized violence, such as the whipping duel (called *tjatjik*) involving groups of participants, or communal battles involving entire villages to settle disagreements over land ownership and use rights (*perang tanding*, or land war); however, various other types of disputes are also likely to lead to violence (Barron and Sharpe 2008; Clark et al. 2004; Downs 1955; Erb 2003). Although there has been a trend in recent years to find or impose other forms of conflict resolution, interpersonal violence is still present in the twenty-first century. For example, over 3 years (2001–2003), 227 violent conflicts were recorded in Flores, resulting in 313 cases of injuries and 117 deaths, generally facilitated by traditional weapons such as knives, machetes, stones, and sticks (Barron and Sharpe 2005). This corresponds to a rate of 2.36 homicides/year for 100,000 inhabitants (taking 1,652,640 as the Flores population size in 2002, Barron and Sharpe 2005), a value on the upper decile of the world distribution of communal and organized armed conflict where none of the parties is the government (UCDP Non-State Conflict Dataset, version 18.1, https://ucdp.uu.se/downloads/#d7). Three sampling sessions were performed (2015, $N = 204$; 2016, $N = 302$; and 2017, $N = 301$) in 174 locations from most regencies (kabupaten) on the islands. Focal individuals were analysed for manual specialization in 2015 and 2016 by Nurhayu et al. (2018), with the conclusion that self-declaration is a reliable and sufficient measure of handedness in Flores and Adonara Islands. In addition to providing their self-declared handedness, focal individuals declared the handedness of their close kin and other family members, resulting in a sample of 10,790 non-focal individuals. When a non-focal individual was later sampled as a focal individual, the handedness attributed by the focal individual was compared to that self-declared by the now-focal individual: in all cases ($N = 99$), an exact concordance was observed. At the beginning of each interview, the participants were informed of the general aim of the study, the type of data to be collected and that the data would only be used anonymously for a scientific purpose. A written voluntary consent was obtained prior to data collection. The interviews were conducted in the Bahasa Indonesia language in the presence of an Indonesian researcher. No financial incentive was provided. Sampling was performed independently of the local proportion of left-handers, although the snowball effect resulted in a higher proportion of left-handers (left-handed neighbours were sometimes solicited by participants as soon as the purpose of the study was disclosed). These non-randomly sampled participants ($N = 32$) and their associated non-focal kin members ($N = 487$) were removed from the final sample because the frequency of the trait studied affects heritability estimate (Lynch and Walsh 1998). After removing individuals with incomplete data ($N = 414$), a final sample of 650 independent pedigrees (see Fig. 1 for an example), corresponding to a total number of 11,490 individuals (focal and non-focal), was obtained. The total number of left-handed subjects was 755 (6.60%), and the total number of right-handed subjects was 10,735 (93.40%). Among individuals of known age (i.e. focal individuals), right-handedness was significantly (Binomial regression, $X^2 = 9.62$, d.f. = 1, $P = 0.002$) associated with older age, with a 0.025 increase of linear unit (i.e., log of odd ratio) for each additional year. For the non-focal individuals, the variation of left-handedness was evaluated across four individual categories with different mean ages (1: grandparents of focal; 2: parents of focal; 3: sibs of focal; 4: child of focal). Left-handedness frequency significantly increased between categories 1 and 2, was not different between categories 2 and 3, and was marginally significantly increasing between categories 3 and 4 (Fisher exact test on 2 × 2 contingency table, $P < 10^{-5}$, $P = 0.63$, and $P = 0.044$, respectively).

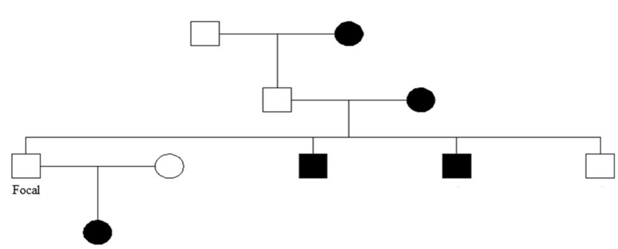

Fig. 1 Example of a pedigree from Flores. Females are represented with a circle, and males are represented with a square. Left-handers are represented by filled symbols, and right-handers are represented by open symbols. 'Focal' designates the sampled individual. Performed with the R package kinship2

Heritability

The total phenotypic variance for handedness was described as: $V_P = V_A + V_R$, where V_A is the additive genetic effect and V_R is the residual variance. The heritability (h^2) of a phenotypic trait is defined as the proportion of phenotypic variance that is attributable to additive genetic effects:

$$h^2 = V_A/(V_A + V_R). \quad (1)$$

Handedness (right/left-handed) was considered a threshold trait. This means that the two options are determined by an underlying continuous distribution, or 'liability' (Falconer and Mackay 1996; Lynch and Walsh 1998), with a threshold of sensitivity. Individuals with liabilities above the threshold are left-handed, whereas those below the threshold are right-handed. Based on this assumption, we estimated heritability for handedness using a pedigree-based animal model. The pedigree was created using the pedigreemm R package. We estimated genetic variance components of handedness with Bayesian inferences using a univariate animal model. Generalized linear mixed models were fitted with Markov Chain Monte Carlo (MCMC) techniques using the MCMCglmm R package (Hadfield 2010). A random effect was introduced, relating individuals to their additive genetic values through the pedigree. Sex was included as a fixed effect. A binomial error structure with a probit link was used, hence $V_R = 1$ (Ødegård et al. 2010; Charmantier et al. 2011). Two distinct functions were used as uninformative or weakly informative prior distributions for V_A : an inverse gamma (Prior1: $V = 1$ and $\nu = 0.002$) or a flat improper prior (Prior2: $V = 1$, $\nu = 0$), as proposed by Hadfield (2015). A MCMC was run for 10^7 steps and sampled every 100 steps after a burning phase of 10,000 steps. The Heidelberg stationarity test was used to evaluate the convergence of the MCMC chain (Heidelberger and Welch 1983). The posterior distribution of the heritability was computed from the posterior distribution of the variance components using Eq. 2.16 of Hadfield (2015); the mean and 95% credible interval were then extracted. The presence of a maternal effect was not tested due to the limited number of cases ($N = 2$) in the pedigrees where maternal-only contribution could be measured, i.e. where a women had children with distinct men. Models with/without an additive genetic variance, or with/without a fixed sex effect were compared using the deviance information criterion (DIC, Spiegelhalter et al. 2002), following Hadfield (2010) and as implemented in MCMCglmm.

Literature data

To find primary data on heritability of handedness, we proceeded in two ways. First, we performed literature searches on accessible databases to find recent publications. Second, to find older data, we scanned cited literature. In addition, inspection of review articles and books from 1957 to 2009 ensured that no major older papers were overlooked (Annett 1964; Clark 1957; Llaurens et al. 2009; McGee and Cozad 1980; McManus 1985, 1991; McManus and Bryden 1992; Porac and Coren 1981). Papers that classify individuals in discrete categories (usually right and left-handers) and provided raw data on handedness over two generations (parents and offspring), or from which raw data could be unambiguously reconstructed, were considered for heritability computation. Cases displaying at least 100 family units were retained. When information was missing (e.g., year of sampling), authors were tentatively contacted to provide the missing information. Papers concerned with the quantification of relative hand performance or preference, e.g., the peg-moving task or handgrip, were not considered. For each estimate, the way in which handedness was measured (writing handedness, handedness for other unimanual tasks, quantitative index, index with 'any left' criterion, self-evaluation), the type of country (industrialized or not), the year of sampling, the sample size, the type of sample (student, general population), and the sample frequency of left-handedness were recorded. For one particular study (Hicks and Kinsbourne 1976), the handedness of the parent generation was measured differently than that of the offspring generation (writing handedness and index, respectively). This study was coded as using writing handedness criteria, although the other possible type of coding (index) or even removing this study did not qualitatively change the results. The university student sample described by Chaurasia and Goswami (in McManus 1985) from Bhopal, India, was considered as originating from an industrialized country. In the university student sample described by Singh and Kundu (1994) from India, individuals were allowed to ascribed the handedness of their relatives using three categories (right, left, ambidextrous), and they reported an unusual proportion of ambidextrous relatives. As the validity of ascribed ambidextry has never been evaluated, these data were not considered.

First, heritability on the observed scale (h^2_obs) was estimated from parent−offspring regression. The classical formula proposed by Dempster and Lerner (1950) to compute heritability on the liability scale was not used, as it leads to overestimates when the left-handed frequency is low (typically lower than 0.25, which is the case for 93% of the present samples), and to larger overestimates when the heritability if large (48% of the samples have h^2 on the liability scale > 0.2, see below), as shown by Van Vleck (1972). For comparison purpose, heritability on the liability scale (h^2_l) was computed using the same method as for the Flores sample, using a pedigree-based animal model. As this method necessitates a large amount of precise pedigrees, pedigrees of simple families were generated for each study, keeping constant the observed left-hander frequency (p_{obs}) and h^2_{obs}. For one estimate, 500 parent−offspring pedigrees were generated. RR, RL, and LL parents were in proportion of $(1-p_{obs})^2$, $2p_{obs}$ $(1-p_{obs})$, and p^2_{obs}, respectively, and each had ten offspring. The probability, for each offspring, to be left-handed was $(1-h^2_{obs})p_{obs}+h^2_{obs}(pp)$, where pp is the left-handedness frequency in parents (0, 0.5, and 1, for RR, RL, and LL parents, respectively). From these pedigrees, heritability on the liability scale was estimated as described above using the MCMCglmm R package. For each study, this process was performed 30 times, and the mean and variance of these 30 estimates were computed. When the true heritability value was close to zero, some MCMC did not converge, and the corresponding estimates were not considered, providing an overall slight overestimate of the mean. To reduce such cases, the number of pedigrees and the number of offspring per family were increased (up to 700 pedigrees, and 30 offspring per family). In order to verify that no bias were introduced, heritability on the observed scale was computed from each set of pedigrees, and compared to the original h^2_obs value. The correlation between the two values was 0.999.

A linear regression was used to assess how estimates of heritability vary according to the type of country (qualitative variable, two modalities: industrial, non-industrial), controlling for the year of sampling (quantitative variable, centred), the frequency of left-handedness (quantitative variable, centred), and the type of handedness measure (qualitative variable, four modalities: writing, other unimanual tasks, quantitative index, index with 'any left' criterion, self-evaluation). Variances of heritability estimates were used as a weight variable. Some studies provided several estimates of handedness heritability using the same data set; thus, study identity was introduced as a random-effect variable and linear mixed models were used (function lmer of lmerTest v3.1-0 R package). The significance of an independent variable was calculated by removing it from the full model and comparing the resulting variation in deviance using a X^2 test (function Anova of the car v3.0-2R package).

Results

Among the 11,490 individuals sampled from Flores and Adonara islands, 755 were left-handers, or 6.6% (Table 1). This proportion remained similar (4.6−8.2%) for the various classes of individuals (parents, child, sibs and spouse's family), suggesting that no sampling bias occurred. The only exception were the focal individuals, with an excess of left-handers (14.6%), and the grandparents, with a deficit of left-handers (2.3%).

Pedigree data from Flores and Adonara Islands were used to estimate handedness heritability using a pedigree-based generalized linear mixed model. The DIC from each model with/without an additive genetic variance and with/without a fixed sex effect were not different for both Prior1 and Prior2, suggesting that the results seem to be prior independent. Models incorporating sex and maternal effect were not retained, as models including only animal as a random effect and sex as a fixed effect were associated with the lowest DIC value (DIC = 3873.9 for Model 2; DIC = 3873.2 for Model 2a, see Table 2). These models generated a converging chain, as confirmed by the Heidelberg stationarity test of convergence ($P=0.73$ for Model 2; $P=0.44$ for Model 2a), with an effective sample size of the mean at 3160 (Model 2 and Model 2a). The traces and density of the posterior distribution of both Prior1 and Prior2 were not different, and the posterior distributions were relatively symmetrical and unimodal (Fig. 2). From Model 2 and Model 2a, heritability estimates were $h^2=0.556$ (95 credible interval from 0.472 to 0.645) and $h^2=0.556$ (95% credible interval from 0.471 to 0.643), respectively. When focal individuals were excluded from the pedigrees to partially control for a residual sampling bias, the heritability estimates were $h^2=0.582$ (95% credible interval from 0.481 to 0.677) and $h^2=0.565$ (95% credible

Table 1 Handedness composition of the members of the pedigrees, relatively to focal individuals

Individuals	R	L	All	Left-handedness frequency
Focal	598	102	700	0.146
Parents	1251	85	1336	0.064
Grandparents	974	23	997	0.023
Child	1393	125	1518	0.082
Sibs	2663	167	2830	0.059
Spouse and spouse' family	828	40	868	0.046
Others (uncles. aunts. cousins. etc.)	3028	213	3241	0.066
All	10,735	755	11,490	0.066

Table 2 Model selection. Models with the lowest Deviance Information Criterion (DIC) are in bold characters

Model	Prior	Fixed effect	Random effect	DIC
Model 1	Prior 1	—	Genetic	3949.082
Model 1a	Prior 2	—	Genetic	3948.469
Model 2	Prior 1	Sex	Genetic	**3873.89**
Model 2a	Prior 2	Sex	Ggenetic	**3873.19**

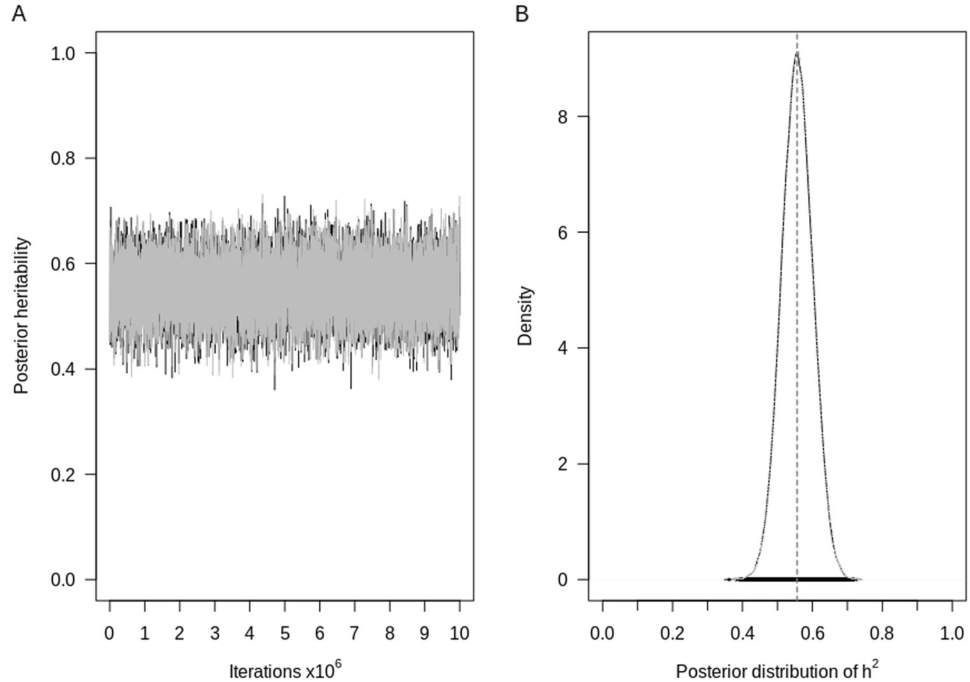

Fig. 2 Heritability posterior distributions of Model2 (with Prior1) and Model2a (with Prior2). **a** Traces of the posterior values along the Markov chain for each prior (black line: Prior1; grey line: Prior2). **b** Density of posterior distribution for Prior1 (black curve) and Prior2 (grey curve). Vertical lines indicate the means

interval from 0.477 to 0.672), for Prior1 and Prior2, respectively.

A total of 18 papers describing 24 studies displayed handedness data over two generations that was sufficient to compute an estimate of heritability. On the overall data set (including the current Flores estimate), heritability on the liability scale ranged from 0.04 to 0.56 (Table 3). This variability was explained by the type of country, with non-industrialized countries (i.e. Flores) displaying a higher heritability value ($P = 1.1 \times 10^{-2}$, Table 4). The weighted mean estimate was $h^2 = 0.20$ (SEM = 0.026) for industrialized countries, and $h^2 = 0.56$ (95% credible interval from 0.47 to 0.64) for the only non-industrialized country. The variability in heritability estimates was also explained by the year of sampling (Fig. 3), with a decrease of heritability of 0.04 ($SE = 1.2 \times 10^{-2}$) per decade. The type of handedness measure, and the frequency of left-handedness had non-significant effect ($P = 0.960$, and $P = 0.761$, respectively, Table 4).

Discussion

The overall analysis of the available data shows that the heritability of direction of handedness is higher in a non-industrialized society compared to that in industrialized countries. The type of handedness measurement and the left-handedness frequency had no significant influence on the heritability estimate.

A relatively high heritability estimate of handedness was found in Flores and Adonara Islands. Indonesia is now categorized as an NIC (newly industrialized country), although most industries are located on Java Island, and the economy of Flores and Adonara is still based on traditional agriculture. Indonesia has recently extended the road and electric networks in Flores, with increasing market integration as a result. Nevertheless, manual work is still intense, and during the sampling sessions, we saw people building houses without the help of any mechanized tools, constructing fishing boats from tree trunks with axes and traditional manual tools, practising fully manual agriculture, manual weaving, etc. Thus, Flores and Adonara could still be considered non-industrialized areas. This is the first time that handedness heritability has been measured in populations where traditional violence is still prevalent or has been prevalent very recently. One frequent type of violence in Flores concerns land disputes (Clark et al. 2004), leading to warfare involving only men. The annual homicide rate in Flores is estimated to be approximately 39 homicides per 100,000 inhabitants (Barron and Sharpe 2005), one of the highest rates recorded among countries worldwide (United Nations Office of Drugs and Crime 2011; 2013). This rate is also higher than the rate calculated for Indonesia as a whole (less than 1 annual homicide per 100,000 inhabitants over the period 2000−2012; United Nations Office of Drugs and Crime 2013).

Several factors could possibly bias the estimate towards higher values, such as an inflated left-hander frequency in the sample. All identified individuals sampled non-randomly (mainly left-handers) were removed from the analysis, although it is possible that some were missed during the recording process in field conditions. To control

Table 3 Heritability estimates from studies displaying raw data

Origin	Year	Sample	Handedness measurement	h^2	SE	Reference
USA (Colorado)	1911–1912	College students	Self-reported handedness	0.55	6.16×10^{-3}	Ramaley 1913
USA (Ohio)	1927	College students	Writing handedness	0.27	1.03×10^{-2}	Chamberlain 1928 (data in Annett, 1973)
USA (Ohio)	1939	College students	Left-hander: any left for ten tasks	0.31	6.79×10^{-3}	Rife 1940 (data in Annett, 1973)
USA (Minnesota)	1957	College students	Left-hander: any left for four tasks	0.18	6.36×10^{-3}	Merrell 1957
USA (Hawaii)	1972–1976	The Hawaii Family Study of Cognition	Writing handedness	0.05	3.99×10^{-3}	Ashton 1982
USA (Texas and New York)	1973–1975	College student	Index: Handedness Inventory (and writing handedness for parents)	0.38	3.96×10^{-3}	Hicks and Kisbourne 1976
USA	1975–1977	General population	Self-reported handedness	0.12	5.49×10^{-3}	Boklage 1981
USA	1975–1977	General population	Self-reported handedness	0.14	6.05×10^{-3}	Boklage 1981
USA (Maryland)	1978–1979	College students	Writing handedness	0.05	2.43×10^{-3}	Spiegler and Yeni-Komshian 1983
USA (Ohio)	1978–1998	College students	Writing handedness	0.1	6.66×10^{-3}	McKeever 2000
USA (Canada)	1979	College students	Edinburgh Handedness Inventory	0.17	4.23×10^{-3}	Bryden 1979
USA (Minnesota)	1979[a]	General population	Edinburgh Handedness Inventory	0.26	8.65×10^{-3}	Carter-Saltzman 1980
USA (Minnesota and Texas)	1979	College students	Left-hander: any left for ten tasks	0.2	6.97×10^{-3}	McGee and Cozad 1980
USA (New York)	1979–1981	College students	Edinburgh Handedness Inventory	0.08	4.09×10^{-3}	Risch and Pringle 1985
USA (New York)	1980[a]	College students and faculty members	Index (Annet and Edinburgh Handedness Inventory)	0.24	5.93×10^{-3}	Leiber and Axelrod 1981
Canada	1980[a]	?	Index (from 5 tasks)	0.04	1.52×10^{-3}	Coren and Porac 1980
UK	1967–1969	College students	Writing handedness	0.26	1.04×10^{-2}	Annett 1973
UK	1967–1969	College students	Left-hander: any left for 12 tasks	0.19	6.58×10^{-3}	Annet 1978
UK	1977	College students	Writing handedness	0.24	6.98×10^{-3}	McManus 1985
UK	1977	College students	Writing handedness	0.24	6.52×10^{-3}	McManus 1985
UK	1977	College students	Writing handedness	0.15	7.48×10^{-3}	McManus 1985
UK	1977	College students	Writing handedness	0.28	4.70×10^{-3}	McManus 1985
UK	1977	General population	Index	0.2	9.91×10^{-3}	Mascie-Taylor, unpublished (data in McManus 1985)
India	1972	College students	Left-hander: any left for ten tasks	0.35	6.51×10^{-3}	Chaurasia and Goswami, unpublished (data in McManus 1985)
Indonesia (Flores and Adonara)	2015–2017	General population	Self-reported handedness	0.56	2.32×10^{-2}	This study

The origin and the population sampled, the year when the data were recorded (Year), the methods of assigning handedness (Handedness measurement), the estimated heritability value on the liability scale (h^2), and its standard error (SE) are shown

[a]When the year of sampling was not indicated, the year of paper submission was used as a proxy

for such a possible residual effect, the analysis was also performed by removing all focal individuals from the pedigrees, although this removal did not lower the heritability estimate, suggesting that a sampling bias is probably not generating an overestimate. Finally, a drastic procedure was performed: all left-handed focal individuals were removed, along with all their associated pedigrees, with a resulting heritability estimate of $h^2 \simeq 0.53$ (95% credible interval from 0.42 to 0.65). This value could thus be seen as a conservative minimum, underestimating the true value as it is computed from a sample from which the frequency of left-handedness has been artificially decreased. Nevertheless, this minimal value is significantly higher than the weighted mean estimate from industrialized countries ($h^2 = 0.20$, SEM = 0.026).

Table 4 Effects of the different variables on the estimate of handedness heritability

Variables	β	SE	X^2 (df)	P value
Intercept	0.192	0.031	—	—
Country type (nonindustrialized)	0.506	0.199	6.49 (1)	$\mathbf{1.1 \times 10^{-2}}$
Left-handedness frequency	−0.091	0.297	0.09 (1)	0.761
Year of sampling	−0.004	1.2×10^{-3}	10.86 (1)	$\mathbf{9.8 \times 10^{-4}}$
Type of handedness measure:			0.30 (3)	0.960
Index	−0.012	0.047	—	—
Self-evaluation	0.029	0.078	—	—
Others	0.02	0.057	—	—

For each variable, the X^2 and P values associated with the chi-square test of the comparison between the full model and the model without the variable are given. Quantitative variables ('Year of sampling' and 'Left-handedness frequency') are centered. For the categorical variables 'Country type' and 'Type of handedness measure', the categories 'Industrialized' and 'Writing', respectively, are included in the intercept. Significant values in bold characters

The sampling year had a negative influence on the estimate of heritability of handedness, suggesting a decrease in the value of heritability over the twentieth century in industrialized societies. This decrease of heritability does not result from a decrease of left-handedness frequency, as the left-handedness frequency was controlled for in the model. In addition, heritability on the liability scale is independent from the frequency of the observed trait (here left-handedness). The evolution of left-handedness frequency could not be properly studied using the present sample, as some studies in Table 3 did not consider randomly sampled individuals and samples rich in left-handers were sometimes considered (e.g., Chamberlain 1928, Annett 1973, McKeever 2000). It has been suggested that left-hander frequency in England decreased in the nineteenth century and then increased during the last century based on the comparison of arm waving in Victorian English films (1897 and 1913) and Google images from the modern population (McManus and Hartigan 2007). Arm waving is not a complex task requiring hand specialization, such as writing or throwing, and has not been considered previously in the various studies on handedness. The way in which arm waving handedness correlates with the other classical measures of handedness, including self-declaration, is currently unknown. It has been suggested that

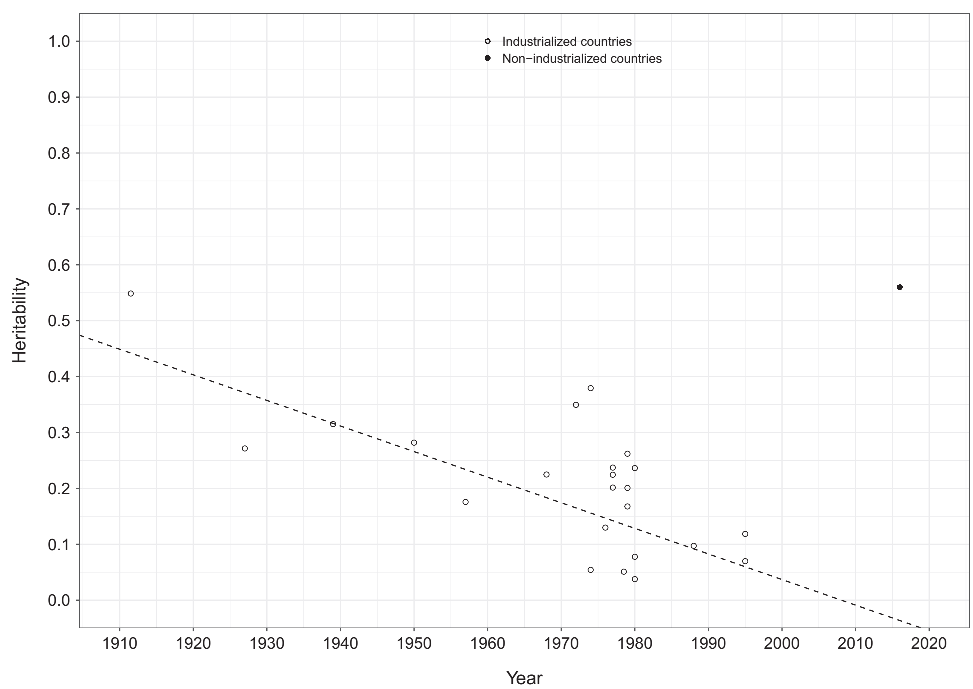

Fig. 3 Heritability estimates from industrialized and nonindustrialized countries. Each circle represents an estimate from a study, or the mean of several estimates from a same study. The regression line for industrialized countries is shown (dotted line)

historical and geographical variations in left-handedness frequency are primarily genetic in origin, rather than due to differences in direct social pressures (McManus 2009). However, the recent evolution of the left-handedness frequency remains a debatable subject due to the variability of methods used to assess handedness and the variability of results concerning the correlation between the various tasks considered (e.g., Milenkovic and Dragovic 2013 versus Briggs and Nebes 1975 or White and Ashton 1976). It is thus possible that the different measures of handedness do not measure the same phenomenon. To better understand that situation, the various handedness studies over the last century should be considered in order to evaluate the evolution of left-handedness frequency for each measure of handedness. This aspect seems less important for the estimation of heritability, as the variability of the various estimates was not explained by the method of measuring handedness.

No maternal effect on handedness inheritance could be evaluated in Indonesia. This was due to the limited number of cases ($N = 2$) in the pedigrees where maternal-only contribution could be measured, i.e. where a women had children with distinct men. A maternal effect on offspring handedness was previously proposed; there was a higher prevalence of left-handedness in children when the mother was left-handed compared to the prevalence when the father was left-handed in a family unit with discordant handedness (see McManus and Bryden 1992 for a review). Whether the maternal effect is geographically variable, or it varies with the type of handedness measure is not known. Most studies reporting a maternal effect used writing as a measure of handedness (e.g., Annett 1973; Ashton 1982; Chamberlain 1928; Spiegler and Yeni-Komshian 1983), although it was also reported when quantitative indexes (e.g., Falek 1959; Harkin and Michel 1988; Risch and Pringle 1985), or ‘any left’ criterion (McGee and Cozad 1980) indexes were used. As this maternal effect seems strong enough to be detected despite the variability of the handedness measurements, it may represent a genuine effect in industrialized countries, possibly mediated by still unidentified cultural or genetic factors. Whether or not these factors are also operating in non-industrialized countries remains to be established.

The genetics of handedness have not yet been fully deciphered (e.g., Ocklenburg et al. 2013; Brandler and Paracchini, 2014; Shore et al. 2016; Güntürkün and Ocklenburg 2017). Major gene models, even when considering various dominance or penetrance levels (e.g., Trankell 1955, Annett 1964; Levy and Nagylaki 1972; McManus 1991; Armour et al. 2014), were found insufficient to account for the inheritance data, suggesting that several interacting genes contribute to the trait. Most of the genetic analyses for lateral preference have been performed in industrialized countries, where the environmental conditions are generally not favourable for the expression of general handedness at the individual level. It is possible that the penetrance of the genes affecting handedness has been modified in industrialized countries, where arm or hand specialization is less needed. The new environmental conditions thus affect the former expression of the trait, although the details of this change in expression are not clear. For example, writing corresponds to a culturally important task in modern societies compared to traditional ones. Writing handedness is prone to cultural influences (Bryden et al. 1993; Mandal 1999; Shimizu and Endo 1983; Teng et al. 1976), thus increasing the environmental variance; the resulting effect is a low estimate of the heritability of writing handedness or a lower heritability estimate when the writing hand contributes to the measure of handedness. Without proper knowledge of the genetics of handedness, it is difficult to infer the various existing environmental interactions and to understand how handedness correlations for various tasks partially decrease in industrialized countries. As a consequence, it is difficult to decide which handedness measure would be rationally valid among single tasks or among various ways to compute indexes from several tasks.

This study presents several limitations. First, it provides only one heritability estimate from a relatively violent and non-industrialized country. The relatively high value could not be unambiguously attributed to a particular variable, such as intense and specialized manual labour. Only additional data from other non-industrialized areas with variable degrees of violence involving only traditional weapons will allow us to form conclusions. Second, the constructed pedigrees relied largely on the collection of indirect data. Although the quality of these indirect data were controlled when non-focal individuals were also sampled as focal individuals (and a 100% concordance was found), some misattribution of handedness for non-focal individuals was still possible, as only 0.91% of non-focal individuals were verified. Removing focal individuals did not decrease the heritability estimate, suggesting that this possible bias remains minimal. It is difficult to assess whether some misattribution will underestimate (left-handers are a minority and more often forgotten) or overestimate (left-handers are conspicuous and more often remembered) the left-handedness frequency and how this modified left-handedness frequency affects heritability estimates. Third, paternity uncertainty could be a possible bias, introducing errors in the pedigrees. We are not aware of non-paternity estimates from Indonesia and specifically from Flores or Adonara Islands. However, the proportion of extra-pair paternity in human populations is very low (Larmuseau et al. 2016); thus, paternity uncertainty is probably not a strong bias, even if it remains a noisy parameter.

In conclusion, the data are consistent with a decrease in handedness heritability following the industrialization process and/or the associated decrease in violence using traditional weapons. The difference in heritability between industrialized and non-industrialized countries suggests that selection of handedness is thus likely to differ between traditional and modern societies. Additional data from other non-industrialized countries, and possibly from areas that do not use modern weapons to settle interpersonal or intergroup disagreements, are required to further evaluate this hypothesis. As the handedness heritability in Flores is at the same level as in industrial countries at the beginning of the twentieth century, it will be interesting to follow in the future how this value evolves according to social changes in Flores, particularly those affecting hand usage (Schaafsma et al. 2012).

Data archiving

The data and R scripts for generating Tables 1, 2, 4, and Fig. 3, are available from the Zenodo open-access repository at https://doi.org/10.5281/zenodo.3460771.

Acknowledgements We are grateful to the Programme Magister Menuju Doktor untuk Sarjana Unggul (PMDSU) 2015 Contract No. 3/E1/KP.PTNBH/2019 from Ministry of Research, Technology and Higher Education to BS, to PHC—Nusantara grant # 41100 WC, to Bernard Godelle for advice, to Jacques David and Anne Charmantier for advice on heritability estimates using the animal model, and to Chris McManus for useful insights on heritability, helpful discussions, and for sharing unpublished data. Heritability computation benefited from the Montpellier Bioinformatics Biodiversity platform supported by the LabEx CeMEB, an ANR "Investissements d'avenir" program (ANR-10-LABX-04-01). This is a contribution ISEM 2019-187 SUD of the Institute of Evolutionary Science of Montpellier.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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